ARBOREAL BEHAVIOR IN THE TIMBER RATTLESNAKE, *CROTALUS HORRIDUS*, IN EASTERN TEXAS

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Abstract.—There have been several recent reports, and anecdotal observations extending back at least to J. J. Audubon, suggesting that the timber rattlesnake (*Crotalus horridus*) is one of the most arboreal members of the genus. Most previous records are of snakes located at heights of less than 5 m. Telemetry studies in eastern Texas have documented more frequent arboreal activity (16.1% of locations of sub-adult snakes) and at greater heights (up to 14.5 m) than previously reported. Unlike previous reports, observations of arboreal activity were restricted to sub-adult snakes (<90 cm SVL), possibly because adult snakes in the current study area are considerably larger than those in other areas where arboreal activity has been documented. Increasing body size and mass may preclude arboreal behavior in larger individuals of this species. Despite considerable speculation on the motivation(s) for arboreal activity in this species, the factors involved remain unclear.

Arboreal behavior in snakes is increasingly recognized as an important aspect of snake ecology (Lillywhite & Henderson 1993). Anecdotal accounts of arboreal activity by timber rattlesnakes (*Crotalus horridus*) date back at least to Audubon (Klauber 1972). In a well known painting by Audubon a timber rattlesnake is depicted attacking Northern Mockingbirds (*Mimus polyglottos*) in a shrub. This painting has elicited considerable discussion concerning the arboreal proclivities of timber rattlesnakes (Klauber 1972).

In recent years, increasing use of radio-telemetry to investigate the biology of timber rattlesnakes has resulted in a proliferation of reports and citations of arboreal activity (Saenz et al. 1996; Coupe 2001; Fogel et al. 2002, Sealy 2002, Bartz & Sajdak 2004). During an ongoing study of *C. horridus* in eastern Texas, Saenz et al. (1996) reported several observations of arboreal behavior. Observations subsequent to the Saenz et al. (1996) report suggest that arboreal behavior, at least by sub-adult individuals, is more frequent in eastern Texas and involves greater heights than previously reported.

A detailed understanding of arboreal behavior in *C. horridus* is limited by the paucity of published records. Saenz et al. (1996) suggested that increasing snake size may limit arboreal behavior in *C. horridus*. Other authors have suggested that arboreal behavior may be

related to basking, avoiding flood waters, ecdysis and foraging (Klauber 1972; Coupe 2001; Fogel et al. 2002, Sajdak & Bartz 2004), and that females may exhibit more frequent arboreal activity than males (Coupe 2001). Additional observations reported here will help to clarify aspects of the arboreal behavior of *C. horridus*.

STUDY AREA AND METHODS

The study area was on and adjacent to the floodplain of the Angelina River in Nacogdoches Co., Texas. Specific study sites were the Stephen F. Austin Experimental Forest located 12 km SW of Nacogdoches (31° 30'N, 94° 47'W), and the Loco Bayou Hunt Club located 15 km WSW of Nacogdoches (31° 31'N, 94° 50'W). Habitat at both sites consisted of bottomland hardwood forest dominated by oaks (*Quercus* sp.), sweetgum (*Liquidamber styraciflua*) and hickories (*Carya* sp.); and adjacent upland forest dominated by loblolly and shortleaf pines (*Pinus taeda* and *P. echinata*), oaks (*Quercus* sp.) and a diverse array of other species. Portions of the bottomland habitats were subject to winter and spring flooding in most years.

Crotalus horridus were captured as encountered during the course of the study, transported to the laboratory, and implanted with SI-2T transmitters (Holohil Systems Ltd.). Transmitters were implanted subcutaneously following the general procedures of Reinert & Cundall (1982) and Weatherhead & Anderka (1984). Snakes were retained in the laboratory, with access to a heating pad, for approximately 7 d following surgery to facilitate healing. Transmitters were replaced at approximately 18 mo intervals.

Following release, snakes were relocated at irregular intervals, GPS locations recorded, and a series of habitat measurements and other data recorded as required for ongoing studies. In instances where individuals were located in arboreal situations, snake height, plant species, diameter at breast height (dbh) of supporting tree, presence of vines and other pertinent observations were noted.

A series of climbing trials using *C. horridus* were conducted on selected trees. Lengths of muscadine grape (*Vitis rotundifolia*) vines 3-6 cm in diameter were occasionally attached to tree trunks to simulate situations noted during climbing events. Observation of subsequent climbing behavior provided some indication of the arboreal abilities of *C. horridus*.

A series of feeding trials were also conducted using Brown-headed

Cowbirds (*Molothrus ater*). Cowbirds were captured in mist nets or box traps, placed in cages with individual *C. horridus* of various sizes, and the snakes' subsequent behavior recorded.

RESULTS

Thirty four *C. horridus* (60-140 cm SVL) were radio-tracked between 1993 and 2000 yielding more than 500 relocations. During this period 12 sub-adult snakes < 90 cm SVL and with a mass < 510 g were relocated a total of 218 times. Eight of these 12 snakes were located in arboreal situations a total of 35 times (Table 1). Each of the four snakes < 90 cm SVL never found in an arboreal location were individuals represented by less than 10 relocation points. Snakes larger than 90 cm SVL, range 90-140 cm, were never observed in arboreal situations, with one exception. An adult male (136 cm SVL) was located in a shrub at heights ranging from 0.5 to 1.2 m on three occasions during a 15 day period. This individual had uncharacteristically occupied a hibernaculum in a bottomland hardwood site prone to flooding. In each arboreal observation the snake had been forced out of the hibernaculum and into the shrub by rising water. This observation is not included in the analyses that follow.

The 35 instances of arboreal behavior represent 16.1% (35 of 218) of total observations of snakes < 90 cm SVL and 17.9% (35 of 196) of observations of those individuals located in arboreal situations at least once. Arboreal behavior was observed in all months from March to October, the general activity period of *C. horridus* in eastern Texas. Of the minimum of 21 separate climbing events, females were involved in 11, males in 10. Contingency table comparison of arboreal relocations vs. total relocations for females (18 of 147, 12.2%) and males (17 of 71, 23.9%) showed a slight, but significant bias favoring males ($\chi^2 = 3.88$. $P < 0.05$).

The heights at which *C. horridus* were located ranged from 0.8 – 14.5 m with a mean of 5.9 m based on the 23 distinct arboreal locations represented. Individual snakes were relocated in the same tree ($n = 9$), occasionally with minor movements ($n = 2$), during subsequent relocations ranging from three to 24 days. There is no way of knowing whether these individuals returned to the ground between observations. Instances where snakes were relocated in the same arboreal location on subsequent days were typically those located at greater heights, however the irregularity of the relocation schedule makes detailed comparisons difficult. In all cases where visual evaluation was possible, snakes were

Table 1. Snake measurements and arboreal behavior data for timber rattlesnakes (*Crotalus horridus*) in eastern Texas.

Snake	Date	SVL (cm)	Mass (g)	Tree Species	DBH (cm)	Snake Height (m)
Female #1	10 Aug. 93	65.4	173.5	*Carpinus caroliniana*	11	3.5
Female #1	5 & 10 May 94	75.4	282.6	*Quercus phellos*	40	7.0 & 9.0
Female #2	14 Sep. 95	87.5	498.8	*Carya* sp.	Small	2.0
Female #3	7 Aug. 96	80.1	450.4	*Quercus laurifolia*	42	14.5
Female #4	29 Sep. 95	78.2	430.3	vines	<2	2.3
Female #4	17 Sep. 96	89.7	503.0	*Quercus lyrata*	37	8.1
Female #5	31 Mar. 99	80.9	257.0	*Ilex decidua*	3	1.0
Female #5[1]	5-14 May 99	80.9	257.0	*Liquidambar styraciflua*	35	6.5
Female #5	18 & 21 May 99	80.9	257.0	*Quercus nigra*	14	6.5
Female #5	24 May & 17 Jun. 99	80.9	257.0	*Quercus muehlenbergii*	46	7.0 & 9.0
Female #5	23 & 29 June 99	80.9	257.0	Unidentified, dead	9.5	3.0
Male #1	2 & 5 Oct. 96	79.1	354.0	*Liquidambar styraciflua*	33	4.5
Male #1	10 Oct. 96	79.1	354.0	*Quercus phellos*	48	4.5
Male #1[2]	1 Mar.-8 Apr. 97	79.1	354.0	*Morus rubra*	23	4.5
Male #2	10 Jul. 97	59.8	127.0	vines	<2	0.8
Male #2	24 Jul. 97	59.8	127.0	*Quercus laurifolia*	13	11.3
Male #2	21 & 28 Aug. 97	59.8	127.0	*Quercus alba*	44	>8.0
Male #2	5 & 8 Sep. 97	59.8	127.0	*Carya* sp.	36	13.5
Male #2	23 Oct. 97	59.8	127.0	Unidentified	3	2.6
Male #2	5 May 98	85.5	508.5	Dead Limbs	?	2.5
Male #3	27 Mar. 97	84.5	488.0	*Quercus laurifolia*	25	2.5

[1] Four observations between 5 May and 14 May 1999.
[2] Five observations between 1 Mar. and 8 Apr. 1997.

coiled or variously extended along branches or in forks of trunks or major limbs. No instances were observed where snakes were coiled around supporting limbs or assumed specific postures to maintain stability in arboreal situations.

The arboreal situations occupied by *C. horridus* varied considerably. Of the minimum 21 distinct climbing events observed, six were situations where snakes were in vine tangles, dead tops of fallen trees, and small saplings or shrubs at heights of 2.6 m or less. In the remaining 15 instances, the snakes were located in substantial trees (9.5 – 48 cm DBH) at heights >2.5 m, often much greater. Vines, smaller diameter trees with low branches, loose bark and leaning trunks potentially facilitated the climbing in six of these instances. However, in the remaining nine instances the snakes were located in canopy or sub-canopy trees (14 – 48 cm DBH) at heights of 4.5 – 14.5 m without obvious characteristics that would facilitate climbing. In the most extreme case, a *C. horridus* was located at a height of 14.5 m at the first major fork of a laurel oak (*Quercus phellos*). The trunk was vertical, with a clear bole, and no vines to facilitate climbing. Access to this site was limited to climbing the vertical trunk or via the canopies of adjacent trees.

Climbing trials with *C. horridus* <90 cm SVL demonstrated limited climbing ability compared to other species (*Elaphe* sp., *Masticophis flagellum*) that typically exhibit arboreal behavior. In cases where smaller branches were available *C. horridus* were able to maneuver slowly along horizontal or inclined branches, bridge between branches, and coil around branches to maintain a stable hold. However, it was not possible to elicit climbing of vertical, or nearly vertical, branches of any diameter, or boles of trees. Throughout these trials snakes gave the impression of awkwardness and hesitancy.

Eighteen laboratory trials were conducted in which birds (*Molothrus ater*) were presented to *C. horridus* of various sizes (range 75 – 104 cm SVL), and subsequent prey capture occurred. In all instances following the initial strike, the snakes maintained a hold on the bird until death of the bird. Time until apparent death of the cowbirds ranged from 54-364 sec with a mean of 188 sec. Feathers appeared to present a substantial impediment to fang penetration, and in several instances the snakes were observed to manipulate the cowbird between their jaws without releasing the bird, often for several min, until they were able to penetrate the feathers with a fang. Smaller snakes that did not immediately achieve an effective bite often had the anterior portion of their body moved

around the cage by the struggles of the cowbirds. The overall behavior of the snakes striking birds was distinctly different from observations of these same snakes preying on a variety of mammalian species where prey was struck and immediately released.

DISCUSSION

Previously published accounts (Saenz et al. 1996; Coupe 2001; Fogel et al. 2002) and included references and communications, Sealy 2002; Sajdak & Bartz 2004; Bartz & Sajdak 2004) suggest that *C. horridus* consistently exhibits arboreal behavior and vindicates portions of Audubon's early observations. However, much remains to be learned about arboreal behavior in *C. horridus*, including prevalence, onto-genetic variation, geographic variation and motivation.

Size appears to limit arboreal behavior in *C. horridus*. Published accounts (Saenz et al. 1996; Coupe 2001; Fogel et al. 2002; Sajdak & Bartz 2004; Bartz & Sajdak 2994; this study) report only five individuals >90 cm SVL demonstrating arboreal behavior: two individuals (99.5 and 112.5 cm SVL) reported by Coupe (2001) without specific details, two individuals (100.5 and 98.0 cm SVL) reported by Bartz & Sajdak (2004) engaged in courtship approximately 1 m above the ground, and the adult male individual reported in this study at modest heights after being forced from its hibernaculum by rising water. The relationship between size and arboreal behavior has not been reported previously, with the exception of Saenz et al. (1996) preliminary report of this study, presumably due to the relatively small adult size of the more northern populations involved in most previous reports.

This study documents more extensive arboreal behavior by *C. horridus*, at least sub-adults, than previously reported (Coupe 2001; Fogel et al. 2002; Sajdak & Bartz 2004; Bartz & Sajdak 2004). Al-though Klauber (1972) characterized *C. horridus* as "among the more persistent climbers," arboreal behavior has been described as uncommon (Fogel et al. 2002), and characterized as frequent, rare, numerous instances, rarely observed (communications in Coupe 2001) without specific details. Only Coupe (2001) provides more specific data, stating that *C. horridus* were observed in arboreal situations during 13.2% of relocations; however, this figure is based on the subset of individuals observed in such situations at least once. In this study sub-adults were located in arboreal situations during 16.1% of relocations, and restricting the data to only those individuals observed in arboreal situations at least once (comparable to Coupe's 2001 data) raises this figure to 17.9%.

Obviously, these data are not directly comparable, primarily because *C. horridus* in the more northern populations rarely reach body lengths at which arboreal behavior becomes extremely rare in eastern Texas.

This study, including the preliminary observations reported by Saenz et al. (1996), is the first to report arboreal activity at substantial heights. Most previous reports are of individuals located at modest heights of 3 m or less, with a maximum of 5 m (Coupe 2001; Fogel et al. 2002; Sajdak & Bartz 2004). In eastern Texas the mean height of arboreal locations was 5.9 m with a maximum of 14.5 m, considerably higher than previously reported for this species. Sub-adult *C. horridus* were regularly located in the lower portions of tree canopies.

Arboreal behavior in *C. horridus* in eastern Texas appears to be more frequent and involve greater heights than is the case in more northern populations. It is important to realize, however, that this comparison is based on sub-adult individuals in eastern Texas, individuals comparable in size to most adults in more northern populations. These comparisons suggest that arboreal behavior is more prevalent in the more southern portions of the range of *C. horridus*. Additional data from a wider geographic range would be desirable.

Coupe (2001) suggested that arboreal behavior might be more prevalent among females. In eastern Texas, males were more frequently observed in arboreal situations based on percent of observations. Overall, currently available data do not demonstrate a consistent difference in arboreal behavior between females and males.

The motivation leading to arboreal behavior in *C. horridus* has elicited considerable speculation but little insight. Of the 23 individuals involved in a minimum of 41 separate climbs and observed on a total of 107 separate days reported in Coupe (2001), Fogel et al. (2002), Sealy (2002), Sajdak & Bartz (2004), Bartz & Sajdak (2004), and this study, two were associated with flood waters, three with ecdysis, one with basking by a gravid female, and four (2 pairs) with courtship. All of these observations were of individuals at heights < 5 m, generally < 3 m. Attaining a preferred thermal regime (basking) could conceivably be associated with several of the above observations and unrecognized in others. However, in Texas obvious basking behavior is rare. Individuals are generally exposed on the forest floor but do not seek open areas, track sun flecks, or show other behaviors that could be associated with basking. Even gravid females, which typically seek heavy cover (hollow logs, debris piles), do not need to bask given the relatively high

average temperatures in the region. Consequently, basking and othe activities noted above can only account for a minority of the observations, and do not appear to be involved in the observations a more extreme heights. These considerations may not even represent the primary motivation that led to the initial climbing activity in all cases.

Avoidance of terrestrial predators is potentially a factor leading to arboreal behavior. If restricted to periods when active foraging is not occurring (ecdysis, post-feeding periods after mobility is regained) benefits might result. However, data or observations that support this hypothesis are not available.

Arboreal foraging is a possibility mentioned by Klauber (1972), Saenz et al. (1996), Fogel et al. (2002), and Coupe (2001). Arboreal foraging was verified in one instance (Sajdak & Bartz 2004) when a was observed capturing a Yellow-bellied Sapsucker (*Sphyrapicus varius*) at a height of 4.5-6 m. Verification of arboreal foraging behavior is difficult because definitive foraging postures in arboreal situations, analogous to those described in terrestrial situations (Reinert et al. 1984), have not been recognized. *Crotalus horridus* preys primarily on endotherms (Clark 2001). Consequently, potential prey available in arboreal situations in Texas are restricted to numerous species of birds, southern flying squirrels (*Glaucomys volans*), squirrels (*Sciurus* sp.) and a limited variety of other small mammals. In a recent compilation of the prey of *C. horridus*, Clark (2001) reported that approximately 7% of recorded prey items were birds, although a substantial number of those identified to species were primarily terrestrial. Squirrels of the genus *Sciurus*, the primary prey of adult *C. horridus* in eastern Texas are often abundant in arboreal situations. However *Sciurus* sp., and in many cases even *G. volans*, are too large for *C. horridus*, of the sizes that typically climb, to handle.

Birds would seem to be the most likely prey of *C. horridus* in arboreal situations. Climbing and predation on birds has been observed in other pitvipers. The shedao pitviper (*Gloydius shedaoensis*) in China, a relatively thick-bodied pitviper where adults average 60-70 cm SVL, actively climbs trees and shrubs and ambushes birds primarily during periods of avian migration (Shine et al. 2002). Striking and holding avian prey, presumably a secondarily acquired trait in Crotalids that prey regularly on mammals (Martins et al. 2002; Stiles et al. 2002), may increase the efficiency of predation on birds. Striking and holding onto avian prey was the strategy used in the report of Sajdak & Bartz (2004), even during a minimum vertical fall of 3 m to a lower branch. Mam-

malian prey that is potentially more dangerous to *C. horridus* is typically released immediately after striking (Chiszar et al. 1982; Stiles et al. 2002). Strike and release would present significant difficulties in trailing prey that could fly, even for short distances, and would presumably be extremely difficult from arboreal situations (Martins et al. 2002). Observations of prey taxa, that present little potential danger or are potentially difficult to trail or handle, that various Crotalids strike and hold include scorpions, fishes, frogs, lizards and birds (Parker & Stotz 1977; Rubio 1998; Hayes & Duvall 1991; Reiserer 2002; Stiles et al. 2002).

The limited climbing abilities of *C. horridus* may limit the possibilities of arboreal foraging to smaller snakes. The apparent lack of behaviors such as coiling around limbs for support, or specialized support postures used by other heavy bodied arboreal species would appear to limit the ability of *C. horridus* to capture and handle prey items in arboreal situations. The report by Sajdak & Bartz (2004) of the *C. horridus* falling to a lower branch during prey capture supports this view. Despite these limitations, foraging remains the most likely general explanation for arboreal behavior in *C. horridus*.

ACKNOWLEDGMENTS

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